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THE CLASSIFICATION OF THE COTINGIDAE (AVES)

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ABSTRACT. The treatment to be given to the Cotingidae in Peters' *Check-list of Birds of the World* is discussed. Both the limits of the family and the best arrangement of the genera within it are problematical, and it is stressed that the system to be adopted must be regarded as provisional.

Previous attempts to classify the family are reviewed. Nine genera are discussed, whose allocation to the Cotingidae has been disputed. Four of these (*Laniisoma*, *Phoenicircus*, *Lipaugus* and *Rupicola*) are considered best retained in the family on available evidence, and five (*Attila*, *Casiornis*, *Laniocera*, *Rhytipterna* and *Xenopsaris*) are considered to belong to the Tyrannidae.

Doliornis and *Zavarornis* are not considered to be sufficiently distinct from *Ampelion* to be maintained as separate genera. Likewise, *Platyparis* is merged with *Pachyramphus*, and *Erator* with *Tityra*.

The sequence of genera adopted indicates a general progression from unspecialized types to highly specialized, sexually very dimorphic frugivores; but it is emphasized that this may not represent an evolutionary progression. Within the genera, there is a marked tendency for closely related forms to replace one another geographically. Many of these are too distinct to be treated as races of one species; moreover, in two cases where there is slight geographic overlap the forms concerned apparently behave as distinct species although they are very similar. To take account of this general situation, liberal use is made of Mayr's concept of the zoogeographical species. On this basis the family is treated as containing 79 taxonomic species and 56 zoogeographical species.

Before his death in 1955, J. T. Zimmer prepared a rough manuscript of the Pipridae, Cotingidae, Tyrannidae, and related families, to constitute volume 8 of Peters' *Check-list of Birds of the World*. The section on the Cotingidae was reviewed in 1957 by James Bond, who made minor modifications, and it was this revised manuscript that was the basis of the classification adopted by Meyer de Schauensee (1966). Volume 8 of the *Check-list*, however, unfortunately remained unpublished.

Having been invited by Melvin A. Traylor, who has accepted responsibility for the final editing of this volume, to revise Zimmer's manuscript of the Cotingidae in the light of recent work, I here discuss the controversial points in the classification of this difficult family at the species level, in particular the affinities of the genera *incertae sedis*, the limits of some of the species, and the sequence to be adopted in the *Check-list*. Zimmer, as is well known, was a meticulous worker with subspecies, and his treatment was reviewed by Bond, as already mentioned. It has therefore seemed unnecessary to alter his arrangement of subspecies except where modification is called for in the light of more recent published reviews. Hence in what follows no mention is made of subspecies except where they are involved in questions of specific status.

The Cotingidae is a notoriously heterogeneous family, and successive systematists have despaired of producing a satisfactory classification of it. About half of the genera are monotypic, and several others are represented by a single superspecies. Many of these are such distinct forms that it is not possible to say to which other genera they are most closely related. Moreover, it has been doubted, by one worker or another, whether about a third of the genera should belong in the family at all. Recently there have been some very useful anatomical studies that have thrown new light on relationships within the family, and within the whole suboscine complex; but even so, it is not yet possible to make anything like a final classification of the family.

What we have to deal with, it seems, is a collection of very diverse evolutionary lines whose common ancestry lies far back in the stock of forest-inhabiting, insectivorous and frugivorous birds that gave rise to the present-day manakins and tyrant-flycatchers, as well as the present-day cotingas. There is no certainty, and probably never will be, that even the "best" cotingid genera may not be more closely related to birds that are now placed in one of the other two families than they are to some other "good" cotingas. Nevertheless, some arrangement has to be made, and it should be based on the best available evidence, and should be justified. It is the purpose of the present paper to justify the treatment to be given to the family in Peters' *Check-list*.

THE LIMITS OF THE FAMILY COTINGIDAE

Sibley (1970) has given a useful historical review of the attempts to classify the passerine birds, and it is not necessary to go over the same ground. For the present purpose it need

only be said that, ever since the foundations of the present arrangement of the passerines were laid by Nitsch, Müller, Garrod, and others, and systematized by Sclater (1888), there has been great uncertainty as to where the dividing lines should be drawn between the three main suboscine families of the New World, the Cotingidae, Pipridae and Tyrannidae (with which are associated the two very small families, Phytotomidae and Oxyruncidae). Recently, moreover, Olson (1971) has widened the controversy by reviving Pycraft's contention that the Old World family Eurylaemidae may be the closest relatives to the Cotingidae. According to this view, the Eurylaemidae and Cotingidae are derived from the primitive suboscine stock, and the Tyrannidae, by implication, are the result of a more recent evolutionary radiation. It seems entirely possible, however, that much of the detailed resemblance between the specialized frugivorous members of the Eurylaemidae and Cotingidae, which Olson stresses, may be convergent; but whether the resemblance is the result of relationship or convergence, it does not resolve the difficulty under discussion, that among the less specialized members of the Cotingidae (as usually considered) there are genera that approach the tyrant-flycatchers and manakins more or less closely.

Olson's suggestion raises an important general point, that it may be incorrect to regard the specialized frugivorous cotingids as the culmination of the adaptive radiation of the family. Previous classifications of the cotingas have usually started with the apparently less specialized types, and have ended with the specialized frugivores such as the fruit-crows and bellbirds, and this is a convenient sequence which is followed here too (p. 13); but it must be admitted to be no more than a matter of convenience. The evolutionary interaction between specialized fruit-eating birds and the fruits to which they are primarily adapted, belonging mainly to a small number of plant families (Snow, 1971b), has obviously been a very long one; in fact, the evolutionary history of the frugivorous stocks may be older than that of the more specialized insectivorous types.

Previous classifications. Sclater, in the *Catalogue of Birds in the British Museum*, vol. 14 (1888), recognized 31 genera in the Cotingidae, dividing them from the Tyrannidae and Pipridae on the basis of tarsal scutellation. The relevant part of the key is as follows:

a. Tarsus exaspidean.

a'. Toes nearly free (as in the *Oscines*).

 Bill incurved, hooked 1. Tyrannidae

Bill straight, pointed 2. Oxyrhamphidae [=Oxyruncidae]
b'. Toes more or less united. 3. Pipridae
b. Tarsus pycnaspidean.
 Bill elongated, compressed,
 not serrated 4. Cotingidae
 Bill short, conical,
 serrated 5. Phytotomidae

In this classification, all three families were distinguished from the Eurylaemidae by the conformation of the manubrium of the sternum, which, as Olson (1971) has since shown, may show considerable intrageneric variation in the characters that have been used to separate families. Although he was aware of the fact that the main artery of the thigh is the sciatic in *Rupicola* and the femoral in all the other cotingas studied, Sclater did not consider this to be of sufficient importance to justify removing *Rupicola* from the family. He placed it in a subfamily, including with it *Phoenicircus* (whose thigh arteries had not been studied and still have not been) for no very convincing reason.

Ridgway (1907), in prefacing his very detailed key to the family Cotingidae, pointed out that the nature of the tarsal scutellation was not so invariable within the families as Sclater supposed. He followed Sclater's arrangement almost exactly, however, the only changes being to replace *Laniisoma* in the family (placed in the Pipridae by Sclater), remove *Laniocera* to the Pipridae, and add to the family eight genera that are now generally considered to be tyrannid and a ninth, *Xenopsaris*, which has subsequently been bandied between the two families. In spite of his *caveat* on the variability of tarsal scutellation, all these changes from Sclater's treatment were made on the basis of this character, except for *Rupicola*, which Ridgway placed in a separate family on the basis of the arteries of the thigh. Ridgway also divided Sclater's *Tityra* into two genera, *Tityra* and *Erator*, largely on the basis of tarsal scutellation.

The next important classification of the family was that of Hellmayr (1929). Again, he followed Sclater and Ridgway closely as far as most genera were concerned. He agreed with Ridgway in including *Laniisoma*, but differed from him in also keeping *Laniocera* in the family. He removed the eight genera of small flycatcher-like birds that Ridgway had brought into the family, as well as *Xenopsaris*. Like Ridgway, he treated *Rupicola* as a separate family. He did not subdivide the genus *Tityra*.

These three classifications agreed in large part, in regard to the genera admitted into the family. Ridgway's sequence, however, departed radically from that of Sclater. Both sequences were simply the result of the keys which they devised, and they do not appear to have been intended to reflect any evolutionary development, such as from more primitive to more specialized types. Thus Ridgway began the family with the peculiar genus *Phoenicircus* and followed it with the very different genus *Laniisoma* simply because the first division of his key dealt with the union (or non-union) of the outer toe to the middle toe.

It is noteworthy that these three authors all questioned the correctness of placing *Attila* (and Sclater also *Casiornis*) in the Cotingidae rather than in the Tyrannidae. Ridgway expressed the same doubts about *Rhytipterna* and *Lipaugus* and the flycatcher-like genera, which he separated from the Tyrannidae "solely on account of the different character of the tarsal envelope."

Meyer de Schauensee (1966) followed Hellmayr fairly closely. He replaced *Xenopsis* in the family, however, with a footnote indicating that it may be tyrannid, and he added the newly discovered genera *Zaratornis* and *Conioptilon*, and the recently described genus *Pseudattila*. In his later book (1970) he made a more important change. As a result of recent anatomical research, he removed five genera and placed them in the Tyrannidae. These were the controversial *Attila* (with *Pseudattila*), *Casiornis*, *Laniocera*, and *Rhytipterna*. He also modified Hellmayr's order of genera in two ways. He placed *Ampelion*, *Zaratornis*, and *Doliornis* later in the sequence, associating them with the other Andean genera *Pipreola* and *Ampelioides* rather than with the eastern Brazilian genus *Phibalura*. Secondly, he placed *Phoenicircus* at the end of the family, after *Procnias*, instead of at the beginning.

The debated genera. The eight genera that Ridgway alone included in the Cotingidae are now generally agreed to belong in the Tyrannidae, and they will not be discussed further (*Microtriccus*, *Ornithion*, *Tyrannulus*, *Idiotriccus*, *Elainopsis*, *Hylonax*, *Ramphotrigon*, *Syristes*). Apart from these, there are nine genera whose position has been debated.

LANIISOMA

Laniisoma was placed in the Pipridae by Sclater (under the name *Ptilochoris*) on the basis of its foot structure and tarsal

scutellation. Ridgway replaced it in the Cotingidae, linking it with *Phoenicircus*, also on the basis of its foot structure. Curiously enough, among the other characters that he listed for these two genera, he gave for *Phoenicircus* "adult males with sixth and seventh primaries shortened, especially the seventh, which is strongly bowed . . .," and for *Laniisoma* "adult males with sixth and seventh primaries normal"; but in fact males of *Laniisoma* have the seventh primary modified, as Sclater noted, though to a much less extreme degree than *Phoenicircus*. Thus *Laniisoma* and *Phoenicircus* agree in structural characters of both wing and foot, though they are very different in plumage. *Laniisoma* has not been dealt with in recent anatomical studies, being rare in collections, and nothing is known of its behavior. Its distribution is similar to that of *Phibalura*, with a south-eastern Brazilian population and restricted populations along the eastern slopes of the Andes. It also resembles *Phibalura* in some points of plumage.

On present evidence *Laniisoma* is best kept in the Cotingidae. It is in accordance with the little that can be inferred about its relationships to place it between *Phoenicircus* and *Phibalura*, but this creates difficulties, as discussed under Sequence.

PHOENICIRCUS

Phoenicircus seems to be a very isolated genus, in spite of the characters shared with *Laniisoma*, as noted above. All recent classifications have placed it in the Cotingidae, though Hellmayr (1929) remarked (footnote, p. 92) that it is "a genus of doubtful affinity, perhaps more nearly related to the *Rupicolidae* or constituting a family by itself." Sclater also linked it with *Rupicola*, in the subfamily Rupicolinae, but on what real evidence is not clear. In his key to the subfamilies the designation for the Rupicolidae, "Tarsi very strong; gressorial," refers only to *Rupicola*; in fact only the crest (very different in the two genera), the presence of modified primaries in the male (but different ones, and many cotingid genera show such modifications) and the general colour serve as a very tenuous link between the two genera.

The anatomy of *Phoenicircus* has not been investigated, and very little is known of its behaviour except that it appears to have some form of communal display (Olalla, 1943). The united toes, the colour of the plumage, and the communal display all suggest that it may be an overgrown manakin. At least, this

possibility deserves as much consideration from future workers as the more usual idea that it is cotingid; but until more is known about the genus it is preferable to retain it in the Cotingidae.

ATTILA

Superficially, its narrow hooked beak, flycatcher-like plumage, general behaviour (Skutch, 1971), and habit of nesting in niches in tree trunks all tend to suggest tyrannid affinities for the genus *Attila*. Sclater, however, following Sundevall, placed it in the Cotingidae, forming a subfamily Attilinae with *Casiornis*, on the basis of the tarsal envelope. Although he expressed doubt about the correctness of this, subsequent authors all kept *Attila* as cotingid, though usually with reservations. Ridgway pointed out that the tarsus is not in fact typical of the cotingas. Meyer de Schauensee (1966) followed the conventional treatment in his 1966 work, but in 1970 transferred *Attila* to the Tryannidae, as a result of Warter's studies of the skull. (Warter's work is not yet published, although cited with a publication date of 1966 in Meyer de Schauensee, 1966: 314, footnote.) The more recent studies of the syrinx by Ames (1971) confirm the tyrannid character of *Attila*, whose syrinx is closely similar to that of *Myiarchus*. It may be noted that these two genera have the same kind of nest-site.

There is little doubt that *Attila* should be removed from the Cotingidae, and placed in the Tyrannidae near to *Myiarchus*. The anatomy of *Pseudattila* has not been studied, but it seems so close to *Attila* (not having been separated as a genus until 1936) that it may safely be placed next to it.

CASIORNIS

Most of what has been said about *Attila* applies equally to *Casiornis*. Structurally it is close to *Attila* (in tarsus, beak, and syrinx [Ames]), but little seems to be known about it in life and its nest has apparently not been found. On present knowledge it seems best to place it close to *Attila* and remove it from the Cotingidae.

LANIOCERA

Sclater placed *Laniocera* in the Cotingidae, while noting that in foot structure it resembles the Pipridae. Ridgway, on the basis of its foot structure (exaspidean tarsus and extensively

coherent toes), placed it in the Pipridae, but it was replaced in the Cotingidae by Hellmayr in spite of its foot structure because of the general similarity of its appearance to *Lipaugus* and *Rhytipterna*. Recent studies of its osteology and syrinx, however, suggest strongly that its correct place is in the Tyrannidae, presumably close to *Attila*. The genus is little known in life, and no nest has been found.

RHYTIPTERNA

There was general agreement in placing *Rhytipterna* in the Cotingidae, close to *Lipaugus*, until Meyer de Schauensee removed it to the Tyrannidae along with the genera *Attila* and associated genera, as the result of recent studies of the osteology and syrinx. This anatomical evidence seems too strong to be set aside.

The very peculiar tarsal scutellation of *Rhytipterna* separates it from all other genera, whichever family it is placed in. Nothing seems to be known of the genus in life, but it may be guessed that the spiky tarsal scutes are in some way connected with its nest-site or even its roosting behaviour. In the former case they might be analogous to the horny processes on the plantar surface of the tarsi of some hole-nesting non-passerines such as jacamars (in which case there would be a further link with *Attila*, a niche-nester), or in the latter case to the tarsal serrations of the tree-roosting *Tinamus*. Field observations on all the genera that are here thought to be close to *Attila* are badly needed.

LIPAUGUS

There has been consistent agreement among systematists that *Lipaugus* is a cotinga, but on the basis of his syringeal studies Ames (1971) has recently suggested that "*Lipaugus* may later be added to this group" (*Attila* and related genera, which must be transferred to the Tyrannidae). The only specimen available for study, however, was damaged, and no firm conclusion was possible.

The two closely related species *L. vociferans* and *L. unirufus* seem to be typical cotingas, so far as they are known in life. Males of *L. vociferans* display in leks (the advertising display being vocal, not visual), and the nest (*L. unirufus*, Skutch, 1969;

L. vociferans, Willis, personal communication) is a minute stick platform such as other medium-large cotingas (*Xipholena*, *Procnias*) build, but no tyrannids so far as known. Moreover, in spite of the dull grey, brown, or greenish plumage of most of the species, *L. streptophorus* has a brilliant magenta collar encircling the anterior part of the body, and Völker (1952) has shown that the pigment in these feathers, as in the red feathers of other cotingids, changes to orange under mechanical pressure.

In summary, the evidence, though scanty, suggests that *Lipaugs* should be retained in the Cotingidae. The peculiarities of the syrinx may well be related to the extraordinary development of vocal display in the genus, and may thus be a specialization rather than an indication of relationship. In this connection it would be interesting to examine the syrinx of a species that has not been reported to have an unusually loud voice, e.g., *L. streptophorus*.

It is not surprising that Hellmayr was impressed by the general similarity of *Lipaugs*, *Laniocera*, and *Rhytipterna*. In addition to their general resemblance they show a remarkable parallelism in geographical variation. In each genus there is a grey form widespread in South America east of the Andes, which is replaced by a chestnut-brown form in Central America and South America west of the Andes.

XENOPSARIS

Sclater placed this genus in the Tyrannidae, as did most authorities of his time, although the single species, *X. albinucha*, was originally ascribed to the cotingid genus *Pachyramphus*. Ridgway placed it in the Cotingidae, noting that its tarsus is not exaspidean, thus not conforming to his main criterion for the Tyrannidae. Hellmayr removed it again to the Tyrannidae, and Meyer de Schauensee replaced it in the Cotingidae. This genus has thus been switched back and forth four times. As Meyer de Schauensee notes, "anatomical investigation is needed to settle the disputed status of this genus," but it is not abundant in collections and its anatomy is still unknown.

If it is a cotinga, it is unique in its habitat; no other member of the family is found primarily in reedbeds and other riverine vegetation, but many tyrannids are. The evidence for the tyran-

nid affinities of *Attila* and related genera shows that undue reliance should not be placed on tarsal characters alone. The evidence is clearly inadequate for a proper decision, but on balance it seems best to place *Xenopsaris* in the Tyrannidae.

RUPICOLA

As mentioned above, Sclater kept *Rupicola* in the Cotingidae in spite of the fact that the main artery of the thigh is the sciatic (as in the Tyrannidae) and not the femoral (as in the other cotingas studied). It is uncertain what weight should be given to this character until the thigh arteries of all the cotinga genera have been studied, but it should be noted that there is apparently no other character which links *Rupicola* with the tyrant-flycatchers rather than with the cotingas. On the basis of the thigh arteries, Ridgway placed *Rupicola* in a separate family, and Hellmayr followed him presumably for the same reason. Subsequent authors have not been consistent: for instance, Meyer de Schauensee (1966) maintains the family Rupicolidae, while Sibley (1970) has replaced *Rupicola* in the Cotingidae.

Sibley's decision was made before any evidence from egg-white proteins was available. Since then, he has analysed the proteins from a fresh egg that I sent him from southern Guyana (Snow, 1971c), and he writes as follows: "Your fine specimen has been 'run' at least three different times with different comparisons, both in isoelectric focusing and also in the standard type of net charge electrophoresis. In all of these it was compared with excellent specimens of *Pachyramphus*, with *Phytotoma*, *Manacus*, at least one or more tyrannid flycatchers, an ovenbird, and an antbird. Without any question, in all of these comparisons, *Rupicola* agrees most closely with *Pachyramphus*. Thus I think it is entirely in keeping with the egg white evidence, which seems to me satisfactory, to include *Rupicola* in the Cotingidae."

If *Rupicola* is retained in the Cotingidae, its isolated position in the family can be given recognition by placing it at the end of the sequence of genera, after the very difficult bellbirds (*Procnias*). The two genera thus represent two distinct types of specialized frugivores, in which the pure fruit diet is associated with marked sexual dimorphism and the evolution of elaborate courtship display.

RECOGNITION OF DEBATED GENERA

Most cotingid genera are so distinct that there has been general agreement about their recognition, even though their affinities may be in doubt. There are, however, a few genera that have been recognized by some authorities but not by others, and these are discussed below. In a family like this, where relationships are so hard to detect and the ratio of genera to species is so high, it seems far more satisfactory to use generic names, when possible, to indicate affinity rather than to emphasize minor differences between forms that are certainly quite closely related.

AMPELION, DOLIORNIS AND ZARATORNIS

Taczanowski in his original description admitted the nearness of *Doliornis* to *Ampelion*, but it was maintained as a separate genus apparently without dissent until Bond (1956) suggested that both it and *Zaratornis* should be merged with *Ampelion*. *Ampelion* and *Doliornis* are both Andean, occurring at high altitudes; they share the same plumage colours (greys and chestnut-browns), and they agree closely in their concealed red-brown nuchal crest. The main structural difference is that *Doliornis* has a narrower and less hooked beak than *Ampelion*. There has been no study of the internal anatomy of *Doliornis*, of which only two specimens are known from a single locality in Peru. It seems most likely that *Doliornis sclateri* has been derived from an isolated fragment of *Ampelion* stock, and the maintenance of the monotypic genus seems unnecessary.

The best treatment of *Zaratornis* is more difficult to decide. Bond recommended merging it with *Ampelion* because of the general similarity of its plumage, especially to that of *A. rufaxilla*. The red-brown nuchal patch is present, though reduced. Its relict distribution in the Andes, like that of *Doliornis*, suggests an offshoot from early *Ampelion* stock. According to J. Farrand, Jr. (personal communication), it is very like *Ampelion* in general behaviour. Farrand writes: "I spent several days at Zarate in the Department of Lima with the late Dr. Maria Koepeke in 1964, and saw the species daily. In its general behavior it is very like *Ampelion rubrocristata*. In a manner very reminiscent of that species it often 'pops up' suddenly onto a dead snag and sits upright, looking about rather nervously. The flight of *Zaratornis* is very similar to that of *Ampelion*, and both species approach a perch flying low and making a final

upward sweep, rather like that of a shrike or kestrel." On the other hand, Lowery and O'Neill (1966) state that its skull, which they have examined, is "so distinct as to preclude making *Zaratornis* congeneric with *Ampelion*." Nevertheless, they place its skull next to that of *Ampelion* in what they describe as a "nicely graded series" of six genera, and the exact differences are not specified. Without knowing to what extent skull structure can be modified in response to differences in feeding behaviour in otherwise closely related forms, it is not possible to weigh the skull differences against the other evidence that suggests close relationship to *Ampelion*. Provisionally, I recommend merging *Zaratornis* with *Ampelion*.

PACHYRAMPHUS AND PLATYP SARIS

The closeness of these two genera has been obvious to everyone who has studied them, though nobody has liked to take the step of formally merging them. Ridgway gave as distinguishing characters the greater size of *Platyparis*, the less extreme specialization of the modified ninth primary in the male, and the more cylindrical, less broad, beak. These hardly seem to warrant the recognition of a separate genus in view of the diversity of size and other characters within the genus *Pachyramphus*. Moreover, the partly concealed white scapular feathers characteristic of *Platyparis* are also present in *Pachyramphus surinamus*. Both genera build gobular, bulky nests, with a side entrance, but that of *Platyparis* is typically suspended from the tip of a drooping branch, while that of *Pachyramphus* is typically supported in a vertical or horizontal fork.

The four species of *Platyparis* are almost completely allopatric (see later, p. 21). They overlap widely with several species of *Pachyramphus*, and their greater size is presumably one of the means by which they avoid competing with them. None of the distinctions seem great enough for generic separation, and they are best united under *Pachyramphus*, the older name, as Bond (1959) has already recommended.

TITYRA AND ERATOR

At first glance the three species in this group (*cayana*, *semifasciata*, and *inquisitor*) seem very close to one another. Ridgway, who laid stress on structural characters that might be used to separate genera, placed the last-named species in *Erator* on the basis of its feathered lores and orbital region.

taxaspidean (not pycnaspidean) tarsus, and broader and flatter bill. Hellmayr and most subsequent authors have preferred to recognise a single genus, although Wetmore (1926, 1927) has upheld *Erator* for the reasons given by Ridgway. It is almost inconceivable that this group of hole-nesting cotingas, whose plumage, modified ninth primary, general proportions, behaviour, and calls are so similar, are not closely related and monophyletic. The presence or absence of areas of bare skin clearly need not be considered of generic importance in the Cotingidae (cf. *Cephalopterus*, *Procnias*); beak shape is presumably adapted to feeding habits (though exactly how in these species is not known); while the difference in tarsal scutellation must be taken to indicate that variation in this character may evolve relatively easily without major modification of other characters.

THE SEQUENCE OF GENERA

As is true for all diverse families, no linear order can express relationships satisfactorily. This would be true even if the relationships were perfectly understood. In the Cotingidae we have a large number of isolated genera whose affinities are quite uncertain, and it seems best to use a sequence that keeps as close as possible to what has been customary while taking account of the more well-based conclusions from recent studies.

Sclater's sequence, as already mentioned, followed directly from his key, and subsequent advances in the systematics of the family make it obsolete. Ridgway's sequence also followed directly from his key, and although it is to this extent artificial it has been generally followed. The reason for this is probably that it seems a more or less natural sequence — except that it starts with *Phoenicircus*, but this genus would be anomalous in any position except the beginning or the end. After this awkward start, the sequence proceeds with five genera (*Laniisoma*, *Phibalura*, *Heliochera* (= *Ampelion*), *Tijuca*, and *Ampelion* (= *Carpornis*)) which are undoubtedly cotingid but unspecialized — that is to say, not specialized towards the large, frugivorous, highly dimorphic types that seem to be the culmination of evolution in the family (but see the *caveat* on p. 3). They are not very specialized in beak shape, and have plumages in which yellows, greens and greys predominate. Moreover, these apparently unspecialized genera are distributed peripherally to the main lowland forest region, which is the headquarters of

most of the specialized frugivores. It is reasonable to regard these genera as closer to the early cotingid stock than the larger, brilliantly coloured fruit-crows and other bizarre forms that are placed towards the end of the generic sequence.

Four genera follow (*Porphyrolaema*, *Cotinga*, *Xipholena* and *Carpodectes*), which consist of medium-sized specialized frugivores with striking colours (purple, wine-red, blue or white) in the male plumage and duller-coloured females. There then follow (omitting the genera that have been placed in the Tyrannidae by all other authors) three genera of small or very small frugivorous forms (*Pipreola*, *Iodopleura*, *Calyptura*), the atiline genera and *Lipaugus*, the tityrine genera, and finally the large and diverse fruit-crows with the very specialized bellbirds (*Procnias*) placed at the extreme end.

Obviously the sequence in which the middle groups should be placed is to a large extent arbitrary, but this order does broadly represent an advancing sequence along the line of specialization for which the family is noted. Probably for this reason, Hellmayr followed it almost exactly (except in so far as he excluded or included the debated genera). Meyer de Schauensee also followed it, except for one major change: he placed *Ampelion* and the two related genera *Doliornis* and *Zaratornis* (the latter not described when Hellmayr wrote) somewhat later in the sequence, before *Pipreola* and after the recently discovered *Conioptilon*.

I believe that the basis of Hellmayr's sequence can be retained, but that some changes are needed in order that it should reflect as far as possible the most likely relationships in the light of recent knowledge. The suggested sequence, with annotations and justification of changes, follows: —

<i>Phoenicircus</i>	}	retained at the head of the list because it is so isolated but, so far as it shows affinities with other genera, may be linked with <i>Laniisoma</i> .
<i>Laniisoma</i>		
<i>Phibalura</i>		
<i>Tijuca</i>		
<i>Carpornis</i>		
<i>Ampelion</i> (including <i>Doliornis</i> and <i>Zaratornis</i>)		shares some characters (especially nuchal crest) with <i>Phibalura</i>

<i>Pipreola</i>	almost certainly closely related; perhaps an offshoot from Andean stock sharing a common ancestry with <i>Ampelion</i> , and more remotely with the four preceding SE Brazilian genera.
<i>Ampelioides</i>	
<i>Iodopleura</i>	of uncertain status; small forest birds not obviously related to each other nor to any other genera; syrinx of <i>Iodopleura</i> of tyrannid type (Ames 1971)
<i>Calyptura</i>	
<i>Lipaugus</i>	probably belong together; not obviously related to other genera
<i>Chirocylla</i>	
<i>Pachyramphus</i> (including <i>Platyparis</i>)	probably fairly closely related (plumage colours, modified ninth primary of males, beak shape); not obviously related to other genera
<i>Tityra</i>	
<i>Porphyrolaema</i>	medium-sized specialized frugivores, sharing some plumage and structural characters; listed together in this sequence by Ridgway and later authors. <i>Xipholena</i> and <i>Carpodectes</i> appear to be closely related, on some characters (Snow, 1971); but Ames has found marked differences in syringeal structure and pits <i>Carpodectes</i> in a different group from the other three, with <i>Querula</i> . Further evidence is needed before upsetting the existing order, which seems satisfactory in other respects.
<i>Cotinga</i>	
<i>Xipholena</i>	
<i>Carpodectes</i>	
<i>Conioptilon</i>	resembles <i>Carpodectes</i> in skull characters, and seems to form a link between the above group and <i>Gymnoderus</i> , which it resembles especially in the great development of powder down (Lowery and O'Neill, 1966).
<i>Gymnoderus</i>	large, mainly frugivorous cotingas, including the so-called fruit-crows. The sequence is the same as that adopted by Ridgway and followed by all later authors, except that <i>Gymnoderus</i> is placed first instead of near the end. This enables <i>Conioptilon</i> and <i>Gymnoderus</i> to be placed together, and does not violate any other known or presumed affinities. The position of <i>Procnias</i> at the end is in accord with its highly distinct syrinx.
<i>Haematoderus</i>	
<i>Querula</i>	
<i>Pyroderus</i>	
<i>Cephalopterus</i>	
<i>Perissocephalus</i>	
<i>Procnias</i>	
<i>Rupicola</i>	

SPECIES LIMITS

A rather large proportion of all genera of cotingas consists of groups of parapatric forms (mainly or entirely allopatric forms that replace one another geographically). The differences between the allopatric populations range from very slight to very marked, thus posing problems of every degree of difficulty in the often arbitrary decisions that have to be made about specific limits. Each case needs to be treated on its own merits, but in fact there is too little evidence in nearly every case to allow a reasoned decision to be made. It is noteworthy, however, that in two cases where very similar forms come together (*Phoenicircus carnifex* and *P. nigricollis*, *Xipholena punicea* and *X. lamellipennis*) they appear to behave as good species, admittedly on very slender evidence (Haffer, 1970). The members of these two pairs are more alike than the members of most other allopatric pairs or groups of cotingas whose specific status is debatable. This should lead to caution in lumping allopatric forms into single species when only an arbitrary decision is possible. It is also very difficult, once one starts to lump allopatric forms, to know where to stop; and awkward situations occur. Logically, if closely related allopatric forms are to be treated as conspecific, *Xipholena atropurpurea* should be treated as conspecific with one of the very closely related species which replace it geographically; but with which? As far as one can tell, it is somewhat intermediate between *punicea* and *lamellipennis* and there is no good reason to link it with one rather than with the other.

For these reasons, I have been conservative in my treatment of allopatric forms, retaining specific status for them unless there seems to be particularly good reason to merge them; and even this involves subjective judgment with which it is easy to disagree. In order to make the classification given in Peters more useful for zoogeographic analysis, groupings of zoogeographic species and possible alternative taxonomic treatments will be indicated in footnotes, where appropriate.

PHOENICIRCUS. The two very similar species, *P. carnifex* and *P. nigricollis*, meet in the region of the lower Tapajos and perhaps the lower Xingu and Tocantins (Haffer, 1970). It seems that they must exclude each other from their respective ranges, but information is quite inadequate to decide the point. There is no evidence for intergradation between them. On present evidence they are best kept as separate species.

PIPREOLA RIEFFERII and P. INTERMEDIA. These two species are closely related, differing chiefly in the terminal tail markings of *intermedia*, which are absent in *riefferii*, and, less strikingly, in other plumage characters. *P. riefferii*, which has a wide range in northern parts of the Andes, is replaced by *intermedia* in Bolivia and most of Peru. Hellmayr (1929) treated them as specifically distinct, since specimens of both, showing no signs of intermediacy, have been collected near to each other in the Department of Libertad, *intermedia* at 2400 m and *riefferii* at 1200 m. Altitudinal data from elsewhere do not show *intermedia* as occurring consistently higher than *riefferii*, and in fact 1200 m is an exceptionally low altitude for either species; in the Department of Amazonas in northern Peru *riefferii* has been collected at 2300–2800 m, while further south *intermedia* had been recorded mainly at 2500–3000 m. Further information is needed on the distribution of these two species where they approach one another, but Hellmayr's opinion regarding their specific status appears sound.

Pipreola arcuata is almost certainly a derivative of the *riefferii*-*intermedia* stock, from which it differs chiefly in its large size and barred underparts. It now overlaps extensively with them.

PIPREOLA AUREOPECTUS, P. LUBOMIRSKII, P. JUCUNDA, and P. PULCHRA. The last three of these obviously form a natural group, as Hellmayr recognized. *P. aureopectus* is more distinct, but *pulchra* forms a clear link between it and the other two. The male of *pulchra* is almost exactly intermediate in its crown colour, and the female is almost exactly like the female of *aureopectus* except for the lack of white apical margins to the wing feathers. All four species agree in the unique combination of red beak, yellow iris, and olive-grey feet. They replace one another from north to south in the Andes, in the order listed, with no overlap so far as known. It seems clear that they should be treated as conspecific.

PIPREOLA FRONTALIS and P. CHLOROLEPIDOTA. The males of these two species at first sight appear very different, since the underparts of *chlorolepidota* are darkish green apart from the throat-patch, and those of *frontalis* are yellow. But the former species retains a small yellow area lateral to the throat-patch, where the feathers are brightest yellow in *frontalis*, and the two species agree in the colour of the soft parts (in the adult male, white or yellow iris, orange or red beak and feet). Moreover, the females are almost identical in plumage. Although they appear to be mainly allopatric, so far as can be told from the

limited records, they overlap in southeastern Ecuador and probably northeastern Peru, and so cannot be considered conspecific; but they have probably speciated comparatively recently.

Iodopleura fusca and *I. isabellae*. These two forms replace one another, so far as known, but there are wide areas where neither has been found. *Fusca* has been found at five localities in Guyana, one in Surinam, and one in eastern Venezuela on the upper Caroni River; the nearest records for *isabellae* are from the upper Orinoco region, the Rio Negro and the middle Amazon (Obidos). Until more is known of the situation in the intervening areas it seems premature to treat them as conspecific, as Hellmayr and others have suggested; they certainly differ more than do *Phoenicircus carnifex* and *P. nigricollis*. It may be noted that *Iodopleura pipra*, the only other species in the genus, which occurs in southeastern Brazil, is also known from two specimens from Guyana. The possibility of long-distance migration by these small aerial cotingas of the treetops cannot be excluded.

Lipaugs vociferans, *L. unirufus* and *L. lanioides*. These three forms replace one another geographically. Hellmayr considered *lanioides* probably conspecific with *vociferans*, but did not go so far as to merge them. No systematist has merged *vociferans* and *unirufus*, although they are almost certainly more closely related than *vociferans* and *lanioides*.

L. vociferans and *L. unirufus* between them occupy almost the whole of the lowland tropical forest region of Central and South America. *L. vociferans* occupies the greater part of the South American range, but does not occur north of the Orinoco (except near its mouth). *L. unirufus* does not extend east of the Magdalena Valley in Colombia. There is thus an area in eastern Colombia and western Venezuela, containing some lowland forest, where neither occurs. The two species are very different superficially, since *vociferans* is all grey and *unirufus* all rufous-brown, but in behaviour and ecology the little evidence there is suggests that they are rather similar, and the colour difference could be based on a small genetic difference. For the reasons given in the introduction to this section I prefer, however, not to treat them as conspecific.

At first sight, *L. lanioides* differs from *vociferans* less than does *unirufus*, but the differences are in fact probably more numerous and important. It is larger, with a browner rump and underparts, and brownish (not grey) wings and tail. It replaces *vociferans* in southeastern Brazil south of 20° S. The

separation at this point involves habitat as well as range, as *vociferans* occurs in lowland tropical forest while *lanioides* is found mainly in subtropical montane forest (but has also been recorded near sea-level, perhaps as a result of vertical migration). Further, although little is known of *lanioides* in life it is hard to believe that it could utter the kind of piercingly loud calls, in leks, that are so characteristic of *vociferans* wherever it occurs. It seems more likely that *lanioides* and the other montane species of *Lipaugus* (*streptophorus*, *fuscocinereus*, *cryptolophus* and *subalaris*) are comparatively quiet birds, with a different social organization from *vociferans* and *unirufus*. Hellmayr's suggestion that *lanioides* and *vociferans* are conspecific thus receives no support in the light of more recent knowledge.

The genus PACHYRAMPHUS. With 11 species usually recognized (15 if *Platyparis* is included), *Pachyramphus* is easily the largest cotingid genus. It is also unique in the family in the amount of geographical overlap between species; in extensive areas up to five or even six species may occur close together, even if not in exactly the same habitats. Some of the species can be placed in groups that constitute zoogeographical species. The arguments for and against recognizing larger specific units than are currently recognized are discussed below.

PACHYRAMPHUS CASTANEUS and *P. CINNAMOMEUS*. *P. castaneus* differs from *P. cinnamomeus* principally in its smaller beak and in the presence of a narrow grey stripe separating the chestnut of the crown from the paler brown sides of the head and neck. Otherwise they are closely similar, and are the only two species in which male and female are alike in plumage. Moreover, both are characteristically found in lowland tropical forest, a habitat avoided by most of their congeners. *P. castaneus* also ranges up into the subtropical zone.

Between them, these two species apparently occupy most of the tropical forest area of South and Central America. In north-western Venezuela and eastern Colombia, their ranges approach closely: *P. castaneus* occurs in the coastal mountains of northern Venezuela, and is replaced by *P. cinnamomeus* round Lake Maracaibo and in the mountains south of Lake Maracaibo. Further south, the potential habitats of the two species are widely separated by savanna country west of the Orinoco, except in the west where a corridor of forest along the eastern foothills of the Andes connects the main forest areas occupied by the two species. *P. cinnamomeus* has apparently occupied

this corridor from the north, as it has been recorded from near Villavicencio, while *P. castaneus* occurs not far to the south, in the forest of the Sierra Macarena.

This geographical replacement suggests that the two species are potential competitors. The morphological differences between them, though slight, seem too clear-cut to warrant treating the two forms as conspecific.

PACHYRAMPHUS RUFUS and **P. SPODIURUS**. Hellmayr pointed out the similarity of these two species and suggested that *spodiurus* might well prove to be the Pacific representative of *P. rufus*. *P. spodiurus* is larger, with a slenderer bill; the male is much darker than *rufus*, but the female plumage is closely similar. The little that has been reported on habitat preference suggests that *rufus* avoids heavy forest, preferring wooded savanna and open woodland; it nevertheless occurs in areas dominated by rain-forest. *P. spodiurus* is also a bird of open woodland, and the absence of records from the very humid coastal forest of northwestern Colombia suggests that it is absent from this area, which thus effectively isolates it from *rufus* to the north.

This is a case much like several others, where two allopatric forms are clearly closely related and it must remain a matter of judgment whether or not they should be treated as conspecific. On balance, and in the absence of any real evidence, it seems that consistency demands that *rufus* and *spodiurus* should receive the same treatment as *castaneus* and *cinnamomeus* and should provisionally retain their specific status.

PACHYRAMPHUS MARGINATUS and **P. ALBOGRISEUS**. These two species agree in many points of plumage, the most conspicuous difference being in crown pattern: the male of *albogriseus* has extensive black on the crown and nape, and the female a brown crown bordered posteriorly with black, forming a patch of the same extent as the male's black; whereas *marginatus* has a small black crown-patch in the male and a brown crown with no black border in the female.

P. marginatus is a bird of lowland tropical forest, east of the Andes. *P. albogriseus* replaces it in limited areas of the Andes, west of the Andes, and in Central America, being found in a variety of habitats, tropical and subtropical. Where the two species approach one another, on the eastern slopes of the Andes of Peru and Ecuador and in northern Venezuela, *P. albogriseus* occurs only at high altitudes and *P. marginatus* in the lowlands.

Again, it seems clear that these two are related, but the little evidence available does not justify treating them as conspecific.

PLATYPSARIS. The close affinity of *Pachyramphus* and *Platyparis*, and the reasons for merging the two genera, have already been discussed. *Platyparis* consists of five forms, usually treated as species, which are almost completely allopatric. Four of these forms between them occupy almost the whole of tropical and subtropical America except some montane and unwooded areas. They clearly constitute a zoogeographical species, but the status of the constituent members is not clear. It is convenient, however, in discussing them to use the four specific names that are in general use. (Unfortunately, the specific name *rufus* is in use in both *Pachyramphus* and *Platyparis*, and when the genera are merged it will be available only for the species currently known as *Pachyramphus rufus*, which has priority.) The fifth form, *P. niger*, occurs only in Jamaica and is rather distinct. The following discussion concerns only the four mainland forms.

P. minor, the central form, occupies the whole of the tropical forest of the Amazon basin and upper Orinoco system. To the south and east, *P. rufus* occurs in a wide variety of more seasonal wooded habitats, tropical and subtropical. These two differ in a number of plumage characters in the male, and less strikingly in the female; they differ also in size. There appears to be no intergradation between them, and moreover their ranges overlap in two areas, in northern Pará and Maranhão in northern Brazil and along the base of the Andes in Peru and Bolivia. These are areas where lowland tropical forest comes into contact with more open vegetation types (N Brazil) or with lower montane woodland (base of Andes). Their ranges also approach closely, and may even interdigitate, along the southern fringe of the main Amazonian forest in central Brazil.

To the northwest, *P. minor* is isolated from *P. homochrous*, also a forest bird, by the savannas of Venezuela and eastern Colombia. Neither species is found in the forested coastal mountains of northern Venezuela. These two forms differ slightly but constantly in both male and female plumage, and are much alike in size.

In Central America *P. homochrous* and *P. aglaiae*, both inhabiting forest or more open woodland according to the habitats available, are separated by a gap between central Panama and central Costa Rica in which neither seems to occur. The populations on either side of this gap are very alike in male plumage,

and in size. The females are more distinct, but some specimens of *aglaiae* resemble female *homochrous* closely. *P. aglaiae* is geographically and individually a very variable species. Webster (1963), in a recent review of its variation, considered it conspecific with *homochrous* by modern standards, and the judgment seems sound.

The evidence does not, however, warrant any further lumping within this group. It is obviously necessary to give specific status to *minor* vis-à-vis *rufus*. No critical test is possible of the status of *minor* vis-à-vis *homochrous*, but the constant plumage differences in both sexes suggest a similar degree of differentiation to that between such species as *Lipaugus vociferans* and *L. unirufus*, whose ranges are also similar to those of *minor* and *homochrous*. It has been argued above that in the absence of evidence to the contrary it is best to give specific status to such forms.

The genus COTINGA. Six of the seven species usually recognized in this genus replace one another geographically: the Central American and northwest South American *amabilis*, *ridgwayi* and *nattereri*; *maynana* of the upper Amazon basin; *cotinga* of the lower Amazon-Guiana region; and *maculata* of eastern Brazil. (The seventh species, *cayana*, is more distinct morphologically and overlaps extensively with *maynana* and *cotinga*.) The first three are very similar to one another, and considered in isolation from the others might reasonably be treated as conspecific. *C. cotinga* and *maculata* are also very similar to one another, and Hellmayr suggested that they might be conspecific. They differ most conspicuously from the Central American forms by the deeper (not turquoise) shade of blue in the male and the more extensive purple below. The sixth form, *maynana*, is at first glance rather distinct from the others. Hellmayr made the rather surprising suggestion that it might prove to be conspecific with the Central American forms, apparently on the basis of its similar shade of turquoise blue.

A more detailed analysis shows that these six forms exhibit a mosaic of characters that link one with another in many different ways (Table 1). The Central American group forms a unit, having in common six of the characters considered, and the two eastern forms constitute another unit, with seven common characters. *C. maynana* is certainly the most distinct form, having four peculiar characters, while none of the others has any character not found in at least one other form. In wing formula, however, *maynana* is closer to *nattereri* than the latter

TABLE 1
Characters of males of six allopatric *Cotinga* species.

	<i>anabilis</i>	<i>ridgwayi</i>	<i>natterii</i>	<i>maynana</i>	<i>cotinga</i>	<i>maculata</i>
Shade of blue	turquoise	turquoise	turquoise	turquoise	deep blue	deep blue
Distribution of purple	throat and belly (two patches)	throat and belly (two patches)	throat and belly (two patches)	small throat patch	extensive patch, throat to belly	throat and belly (two patches)
Colour of feather bases	black	black	black	pinkish purple	black	black
Under-wing	black	black	black	extensive white	black	black
Secondaries and greater covers	blue-edged	blue-edged	blue-edged	blue	black	black
Wing tip: —	abbreviated	normal	normal	normal	abbreviated	abbreviated
Length of 7th primary primaries 7-10				7th and 8th slightly notched	9th and 10th attenuated	9th and 10th attenuated
Eye colour	brown	brown	brown	yellow	brown	brown

is to the other two of the Central American group. Similarly, *amabilis* of the Central American group resembles the two eastern forms, *cotinga* and *maculata*, in its abbreviated 7th primary, while *ridgwayi*, the remaining member of the Central American group, approaches them in the modification of its two outer primaries (but not in its 7th primary, which is normal).

It seems probable that the common ancestor of these six forms — perhaps during a period of contraction of the forests — was divided into a number of isolated populations, which evolved a number of small but consistent differences to which no obvious adaptive significance can now be attributed. The forest refuges suggested by Haffer (1970) provide obvious origins for five of the forms: *amabilis* in the Caribbean (Costa Rica) refuge, *nattereri* in the Chocó refuge, *maynana* in either the Napo or the East Peru refuge, *cotinga* in the Guiana refuge, and *maculata* in the southeastern Brazilian refuge. The sixth form, *ridgwayi*, presumably evolved in a small forest refuge on the Pacific coast of Costa Rica and Panama, to which it is still confined. The rather exact geographical replacement of one form by another, and lack of any evidence of morphological intergradation, suggest that they have reached specific status to the extent of being reproductively isolated, but that they are still not able to penetrate one another's ranges.

In spite of the unequal differentiation of these forms, and the fact that they fall into two groups, with one isolated form, it is probably best to treat all six as species, as has been the usual practice.

The genus XIPHOLENA. The status of the three forms has already been discussed, with the reasons for keeping them as three separate species.

The genus CARPODECTES. This genus consists of three allopatric forms, of which two (*nitidus* and *antoniae*) are very similar to one another while the third (*hopkei*) is a good deal more distinct. There is no doubt that together they constitute a zoogeographical species, but it is less clear whether they should be treated as one, two or three species. All three courses have been adopted or advocated. Slud (1964), however, gives some reasons for keeping *nitidus* and *antoniae* separate, and if this is done *hopkei* must also be given specific rank. Such a treatment is in accord with the general policy adopted for other groups, as discussed above.

The genus CEPHALOPTERUS. In accord with the general

policy adopted, as discussed above, the three allopatric forms of umbrellabirds should be kept as separate species. The differences between them are at least as great as the differences between the overlapping forms of *Xipholena* and *Phoenicircus*.

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APPENDIX

Annotated species list of the Cotingidae; treatment to be adopted in Peters' *Check-list of Birds of the World*.

(Zoogeographical species bracketed)

Phoenicircus carnifex	See discussion, p. 16
Phoenicircus nigricollis	
Laniisoma elegans	
Phibalura flavirostris	
Tijuca atra	
Carpornis cucullatus	
Carpornis melanocephalus	
Ampelion rubrocristata	
Ampelion rufaxilla	
Ampelion sclateri	Formerly <i>Doliornis sclateri</i>
Ampelion stresemanni	Formerly <i>Zaratornis stresemanni</i>
Pipreola riefferii	See discussion, p. 17
Pipreola intermedia	
Pipreola arcuata	
Pipreola aureopectus	Includes <i>lubomirskii</i> , <i>jucunda</i> and <i>pulcha</i> (p. 17)
Pipreola frontalis	See discussion, p. 17
Pipreola chlorolepidota	
Pipreola formosa	
Pipreola whitelyi	
Ampeliooides tschudii	
Iodopleura fusca	See discussion, p. 18
Iodopleura isabellae	
Iodopleura pipra	
Calyptura cristata	
Lipaugus subalaris	
Lipaugus cryptolophus	
Lipaugus fuscocinereus	
Lipaugus vociferans	See discussion, p. 19
Lipaugus unirufus	
Lipaugus lanioides	
Lipaugus streptophorus	
Chirocylla uropygialis	
Pachyramphus viridis	
Pachyramphus versicolor	

Pachyramphus spodiurus	See discussion, p. 20
Pachyramphus rufus	
Pachyramphus castaneus	See discussion, p. 20
Pachyramphus cinnamomeus	
Pachyramphus polychoterus	
Pachyramphus marginatus	See discussion, p. 20
Pachyramphus albogriseus	
Pachyramphus major	
Pachyramphus surinamus	
Pachyramphus aglaiae	Includes <i>homochrous</i> ; see discussion, p. 21
Pachyramphus minor	
Pachyramphus validus	
Pachyramphus niger	
Tityra cayana	
Tityra semifasciata	
Tityra inquisitor	
Porphyrolaema porphyrolaema	
Cotinga amabilis	Possibly the first six species could be
Cotinga ridgwayi	considered as one zoogeographical
Cotinga nattererii	species (p. 22).
Cotinga maynana	
Cotinga cotinga	
Cotinga maculata	
Cotinga cayana	
Xipholena punicea	See discussion, p. 24
Xipholena lamellipennis	
Xipholena atropurpurea	
Carpodectes nitidus	
Carpodectes antoniae	See discussion, p. 24
Carpodectes hopkei	
Conioptilon mcilhennyi	
Gymnoderus foetidus	
Haematoderus militaris	
Querula purpurata	
Pyroderus scutatus	
Cephalopterus glabricollis	See discussion, p. 25
Cephalopterus ornatus	
Cephalopterus penduliger	
Perissocephalus tricolor	
Procnias tricarunculata	All four <i>Procnias</i> species are closely
Procnias alba	related and replace one another al-
Procnias averano	most completely (Snow, in press)
Procnias nudicollis	
Rupicola rupicola	
Rupicola peruviana	

Total: 79 taxonomic species
56 zoogeographical species